A dynamic model of feed intake regulation in dairy cows. Model description

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ABSTRACT

A dynamic, mechanistic and deterministic model of feed intake regulation in dairy cows is described. The model is based on a conceptual model of feed intake regulation involving an interplay between rumen function and energy transactions. Two interconnected submodels are included, the rumen submodel (RS), adapted from a previously developed rumen model and the feed intake regulation submodel (FIRS). From RS rumen digesta load in terms of kg of NDF is calculated. FIRS not only describes the feed intake regulation but also the digestion, absorption and flow of nutrients beyond the rumen. Energy transactions in the model are related to the simulated difference between the capacity to use energy and the intake of metabolized energy. In the model, energy outputs of the animal include not only the energy needed for maintenance and milk production but also the energy needed to support a genetically determined time course of body reserves. Body reserves, both the absolute level and the rate of mobilization are considered in the regulation of feed intake. A preliminary evaluation of the model behaviour for a typical diet and animal inputs showed predicted values within expected values for feed intake, body condition score and body weight.

KEY WORDS: model, evaluation, intake regulation, body reserves, dairy cows

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INTRODUCTION

Prediction of feed intake in ruminants is of major economic importance. This has led to the formulation of many mechanistic intake prediction models in ruminants, either standing alone or as part of whole animal models or as a component of ruminant livestock production systems models, during the last two decades. However, a recent analysis of some of the published models revealed serious drawbacks not only in the concepts and hypotheses on which they are based, but also in their mathematical implementation (Pittroff and Kothmann, 2001). Another conclusion from this paper is that almost all feed intake prediction models for cattle are based on the bi-phasic hypothesis of intake regulation (physical by fill in reticulorumen or physiological by energy demand) which has been rejected as a valid hypothesis through literature reviews (Weston, 1996; Pittroff and Kothmann, 1999) or from experimental work (Rinne et al., 2002).

The size of body reserves and its variation through the lactation cycle is broadly recognised by both its economic significance in terms of feed management and by the health status and reproductive performance of the animal. Body reserves and/ or its variation has only been exceptionally included into a few mechanistic feed intake prediction models (Sanders and Cartwright, 1979; Williams et al., 1989; Mertens, 1994) and when included it was done in a highly divergent manner (Pittroff and Kothmann, 2001).

The objective of this work was to develop a dynamic, mechanistic and deterministic model that will describe the regulation of feed intake in lactating dairy cows in which the physical and metabolic signals that regulate the initiation or cessation of feed intake are integrated.

MODEL DESCRIPTION

The proposed feed intake regulation model (FIRM) includes to interconnected submodels, the rumen submodel (RS) and the feed intake regulation submodel (FIRS). A version of the rumen submodel with a constant value of intake has been published previously (Petruzzi et al., 2002). It describes the digestion and flow of nutrients from the rumen and gives information to the FIRS about the status of nutrient pools in the rumen as well as the flow of different nutrients out of the rumen. The version of RS connected to FIRS is adapted to work on discontinuous feed intake.

The FIRS describes not only the mechanism of intake regulation in the dairy cow but also describes the digestion, absorption and flow of nutrients beyond the rumen and updates information about the dairy cow like body weight and body condition score among other variables.

The mechanism of feed intake regulation in the FIRS is based on the conceptual model of feed intake regulation proposed by Weston (1985, 1996) and basically involves an interplay between rumen function and energy transactions. This conceptual model assumes that the capacity of the ruminant to dispose of energy is the driving component of the system constituted by the sum of the energy needed for maintenance, growth, reproduction and milk production. This capacity is reduced when constraints from the diet or from the environment are imposed to the animal. Certain constraints imposed by the forage prevent the animal to meet the capacity of energy use generating an energy deficit in the animal, which in turns generates hunger signals directly related to the magnitude of the deficit. A direct relationship is assumed between the clearance rate from the rumen and the amount of rumen digesta. This digesta load generates satiety signals, which are also in direct relation to the magnitude of the load once a threshold value is reached. When these signals more than balance the hunger signals derived from the energy deficit the feeding drive is overruled.

No experiments were carried out to develop this model and therefore, parameter values are derived entirely from existing data, published as well as unpublished. Abbreviations, description and units of the variables and the constants used in the FIRS are given in Tables 1 and 2, respectively. The Appendix describes all the equations used in the FIRS model. Along the paper, bold numbers between brackets refer to the equation number in the Appendix and italic type letters between brackets refer to the variable or constant abbreviations. The model is developed using the graphical modelling software Powersim[®], version 2.5 (1996). Runge-Kutta 4th order integration method is used for the numerical solution of the differential equations with a time step of 0.2 h. Energy transactions are given in MJ units. All flow rates are expressed in units of mol carbon (C), mol nitrogen (N), MJ or kg per hour or day. The simulation period is given as an input.

The energy deficit in the animal

Energy deficit is the term proposed originally by Weston (1985, 1996) to relate the energy transactions with digesta load in his conceptual model. It is estimated as the capacity to use energy minus energy intake.

In the FIRM, energy difference (E_diff) is the term used to relate the energy transactions with digesta load and equation (1) represents the calculation of this term. Energy difference is computed as the difference between an energy balance calculated by the model ($E_balance$) and an optimum energy balance determined from a standard curve of corporal condition ($E_bal_optimum$) plus a factor adjusting this difference according to the initial and actual value of body condition of the dairy cow (Fac_BCS).

TABLE 1

Code	Description	Unit
Ab_AC_HG	Absorption of acetate from the hindgut	mol C h ⁻¹
Ab_BU_HG	Absorption of butyrate from the hindgut	mol C h ⁻¹
Ab_PR_HG	Absorption of propionate from the hindgut	mol C h ⁻¹
Adjust_Act	Effect of actual BCS of the animal on feed intake	MJ h ⁻¹
Adjust_Ini	Effect of BCS of the animal at beginning of the lactation on feed intake	MJ h ⁻¹
Amino_acids	Absorption of amino acids in small intestine	mol N h ⁻¹
BCS_optimum	Optimum BCS of the dairy cow in BCS units	
BCSC_M	Body Condition Score Change calculated by the model	
BCSC_optimum	Optimum BCS change	
CH4_HG	Production of methane in the hindgut	mol C h ⁻¹
CO2_HG	Production of carbon dioxide in the hindgut	mol C h ⁻¹
DХ	Delayed information of the variable X. The value is	Units of
	delayed by 24 h unless otherwise stated	variable X
Daily_Preg_E_Ret	Daily Net Energy retained in foetus	MJ d ⁻¹
DE	Digestible energy	MJ h ⁻¹
Der_Load	The derivative of the variable <i>Rumen_load</i>	kg h ⁻¹
DMI	Rate of dry matter intake	kg DM h ⁻¹
E_bal_optimum	Energy balance optimum according to an optimum BCS curve	MJ h ⁻¹
E_balance	Energy balance (net energy for body gain)	MJ h ⁻¹
E_BCS_h	Energy contained per unit of BCS change	MJ BCS ⁻¹
E_diff_h	Energy difference (Capacity to use E - Useful E intake)	MJ h ⁻¹
Endog_protein	Secretion of endogenous faecal protein	mol N h ⁻¹
EV Milk	Energy value of milk	MJ kg ⁻¹
Fac BCS	Influence of BCS on feed intake	MJ h ⁻¹
Faecal C	Faecal C excretion	mol C h-1
Faecal E	Excretion of faecal energy	MJ h ⁻¹
Faecal N	Faecal N excretion	mol N h ⁻¹
Fatty acids	Absorption of fatty acids in the small intestine	mol C h-1
Feed intake	Rate of dry matter intake	kg d ⁻¹
Fermentable HG	Fermentable substrates in the hindgut	mol C h ⁻¹
GE intake	Gross energy intake	MJ h ⁻¹
Glucose	Absorption of glucose in the small intestine	mol C h ⁻¹
HE	Total heat production	MJ h ⁻¹
HE Preg	Heat Energy due to pregnancy	MI d ⁻¹
	Lactation time (days after calving) during the simulation	wij u
Lactation_time	period	D
L1p1d_HG	Entrance of fatty acids into the hindgut	mol C h ⁻¹
Lipid_SI	Entrance of fatty acids into the small intestine	mol C h ⁻¹
Load_Reg	This variable takes the value zero when rumen load allows for eating. Otherwise, the value is 1	

Abbreviations, description and units of the variables used in the feed intake regulation model

	5

TABLE 1 continued

Code	Description	Unit
0000	This variable takes the value zero when the variable	0.111
Load RegA	<i>Load</i> is decreasing and is below a Lower limit.	
_ 0	Otherwise, the value is 1	
	This variable takes the value zero when the variable	
Load_RegB	load is constant or increasing and is below an upper	
	limit	
Lower	Lower limit for rumen digesta load	kg
M_Daily_Preg_E_Ret	Metabolizable daily energy retained in foetus	MJ d ⁻¹
ME	Metabolizable energy	MJ h ⁻¹
Methane_E	Total production of methane energy	MJ h ⁻¹
Milk_E	Total energy in milk	MJ d ⁻¹
MY	Daily milk yield	kg d ⁻¹
	Daily milk yield reduction due to pregnancy. Effects	
MY_Preg_Red	of pregnancy on MY starts in week 18 of pregnancy	kg d ⁻¹
	(126 days)	
NDF_SI	Entrance of NDF into the small intestine	mol C h ⁻¹
OtherCHO_SI	Entrance of other carbohydrates fraction into the small intestine	mol C h-1
Protein HG	Entrance of protein into the hindgut	mol N h ⁻¹
Protein SI	Entrance of protein into the small intestine	mol N h ⁻¹
PW	Weeks since conception	week
RBF Optimum	Optimal backfat during the lactation period	mm
Rumen load	Mass of total NDF in the rumen.	kg
Starch SI	Entrance of starch into the small intestine	mol C h ⁻¹
Sugar SI	Entrance of sugar into the small intestine	mol C h-1
Sugar starch HG	Entrance of sugar and starch into the hindgut	mol C h-1
	Total Net Energy retained at time t in the gravid foetus	M
Iotal_Preg_E_Ret	in cattle	IVIJ
TPR	Total NDF Particles in the rumen	mol C
Upd_BCS	Actual BCS of the dairy cow. Value updated daily	
Upd_BW	Updated body weight	kg
Upper	Upper limit for rumen digesta load	kg
Urinary E	Excretion of urinary energy	MJ h ⁻¹

Determination of energy balance

For the estimation of the energy balance $(E_balance)$ (2) in the model, metabolizable energy (ME) (3) is determined first and then from this, the energy produced as heat, and the energy needed for pregnancy and milk production are deduced to obtain the energy balance. Total energy input in the model (GE_Intake) (4) is estimated as the product of the rate of dry matter intake (DMI) of the ration and the content of gross energy of the diet (GE). This last value is depending on diet

TABLE 2

Abbreviations, description and value and units of the constants used in the feed intake regulation model

A1.1	Description	¥7.1 .	TT. St.
Abbreviation	Description	Value	Units
	Scaling coefficient to express different milk	32.1	
a_l	yield potentials. Values for first, second and	44.9	
	third or more parities	52.8	
Alfa1	Constant in the calculation of Upper	4.15	
Alfa2	Constant in the calculation of Upper	4	
Alfa3	Constant in the calculation of Upper	0.925	
Alfa4	Constant in the calculation of Upper	1.3	
Alfa5	Constant in the calculation of Upper	1.9	
	Factor <i>a</i> in Coulon (1995) equation for	4 2 4 9	
-) (D	reduction in MY due to pregnancy. Values	4.248	
aMK	for primiparous and multiparous low or high-	2.571	
	producing dairy cows, respectively	3.839	
	Rate at which milk vield increase to a peak.	0.0694	
b 1	Values for first, second and third or more	0.0916	
	parities	0.0888	
	Factor b in Coulon 1995 equation for		
	reduction in MY due to pregnancy Values	-0.08	
bMR	for priminarous and multiparous low or high-	-0.035	
	nroducing dairy cows respectively	-0.094	
Body weight	Initial body weight of the dairy cow	Input	kα
Butterfet Mill	Butterfat content in milk	Input	a ka ¹ milk
Dutternat_wink	Butteria content in milk	11put	g kg milk
. 1	Kate of decline of Wilk Yield	0.00218	
c_1	values for first, second and third or more	0.00322	
GIGD' 4 W	parities, respectively	0.00393	
Calf_Birth_W	Call birth weight for Holstein breed	45	kg
Conception Day	Stage of lactation at the time of conception	92	d
	(Days)		
Cte_137	Constant in the calculation of <i>Adjust_Ini</i>	0.0025	
Ctel	Constant in the calculation of <i>Sigm1</i>	0.000002	
Cte3	Constant in the calculation of <i>Sigm1</i>	2.84	
Day1	Length of the day in the model	24	h
Diff	Difference between Upper and Lower limit for	0.6	kα
	rumen digesta load	0.0	ĸg
Eating	Rate of dry matter intake during eating	3.3	kg h ⁻¹
GE	Gross energy in feed dry matter	Input	MJ kg ⁻¹
	Degree of maturity of milk production system	0.206	
Go	at calving. Values for first, second and third or	0.245	
	more parities, respectively	0.089	
Ini Lact time	Lactation time at the beginning of the simulation	Input	D
	Initial BCS of the dairy cow at the beginning		
Initial_BCS	of the simulation period	Input	
K_BCS	Factor used in calculation of Adjust Actual	100	

Protein Milk

			continued
Abbreviation	Description	Value	Units
K_EP	Fractional rate constant of endogenous protein	0.2856	Mol N kg DM ⁻¹
K_HE	Factor used in calculation of HE	0.08	
K_UE	Fractional rate constant of gross energy lost as urine	0.04	
Lact1	Constant in the calculation of RBF_Optimum	22.069	
Lact2	Constant in the calculation of RBF_Optimum	0.236	
Lact3	Constant in the calculation of RBF_Optimum	0.00201	
Lact4	Constant in the calculation of RBF_Optimum	6 10-6	
Lact5	Constant in the calculation of RBF_Optimum	6.32 10-9	
Lactose_Milk	Lactose content in milk	Input	g kg ⁻¹ milk
Parity	Parity number of the $cow (1, 2 \text{ or } 3)$	Input	
Peak_MY	Peak Milk Yield (default = 0)	Input	kg d ⁻¹
Pot_MY	Potential annual milk yield (305 DIM) (default = 0)	Input	kg y ⁻¹

TABLE 2

composition and is given as input to the model at the beginning of the simulation. From the estimated gross energy intake, the energy losses in faces (*Faecal E*), urine (Urinary E) and methane (Methane E) are subtracted to calculate ME.

Input

g kg⁻¹ milk

Crude protein content in milk

Faecal E(5) is the sum of the energy contained in faeces in carbon and nitrogen compounds. These energy values are estimated as the product of the respective flows of C and N compounds (*Faecal C* and *Faecal N*) and the corresponding heat of combustion (0.546 MJ mol⁻¹ C and 23.7 MJ kg⁻¹ protein, respectively). Faecal $C(\mathbf{6})$ is obtained by summing all carbon fractions entering the hindgut minus the absorption and disappearance of short chain fatty acids (SCFA) and fermentation gases produced in the hindgut. No digestion of NDF is assumed in the small intestine (SI), therefore the amount of NDF entering the hindgut (NDF SI) (7) is the same amount of NDF leaving the rumen. For determination of NDF as well as all other nutrients and microbial fractions passing to the duodenum, see Petruzzi et al. (2002).

The fraction of other carbohydrates (cell wall carbohydrates other than NDF, i.e. pectins etc.) entering the SI (OtherCHO SI) (8) corresponds to the sum of the two outflows from rumen of the other carbohydrates fractions and the corresponding proportion of other C fraction (0.0937) from the microbial C passage out of rumen. As for NDF, no digestion of the other carbohydrates fraction is assumed in SI.

The starch and sugar fractions entering SI (Sugar SI and Starch SI) (10 and 11, respectively) from the reticulorumen are partly digested and absorbed as glucose (*Glucose*) (12), and the rest enters the hindgut (*Sugar_Starch_HG*) (9). The rate constant of digestion of sugar and starch in SI (0.884) as well as the rest of the rate constants of digestion and absorption of the different nutrient fractions in SI and hindgut were obtained from the model Karoline (Danfaer, 1998). Both models, the actual version of Karoline and FIRM were run with the same diet and the mentioned postruminal rates of absorption and digestion of nutrients in FIRM were adjusted to match results from the Karoline model.

Lipids entering the SI (*Lipid_SI*) (14) are constituted by fatty acids from dietary origin not digested in rumen and by the proportion of fatty acids in microbes (0.1817) flowing out of the rumen. Most of these fatty acids (83.3%) are absorbed from the SI in the model (15). The remaining fraction (*Lipid_HG*) (13) is the fatty acids entering the hindgut.

The protein flow into the hindgut (*Protein_HG*) is calculated as the protein entering the SI (*Protein_SI*) plus the undigested endogenous protein (*Endog_protein*) minus the fraction of protein digested in SI and absorbed as amino acids (*Amino_acids*) (16). The protein entering the duodenum (*Protein_SI*) is the sum of microbial protein and undegraded dietary protein (17). *Endog_protein* in the model is a function of feed intake (18). The digestion rate constant of protein in the small intestine is taken as 0.735 (19).

All C fractions (except *Lipid_HG*) entering the hindgut and the C contained in dietary and microbial protein flowing into the hindgut constitute the fermentable C fraction (*Fermentable_HG*) (20) and from this the different SCFA and fermentation gases are produced (21 to 25). Rate constants for the production and absorption of acetate, propionate, butyrate, methane and carbon dioxide are 0.0813, 0.0355, 0.0242, 0.0158 and 0.0382, respectively, estimated from the model Karoline (Danfaer, 1998).

Faecal_N (26) is N contained in protein entering the hindgut plus the net difference between urea uptake and ammonia absorption in the hindgut (0.184 mol N h^{-1}), estimated from the Karoline model.

Total energy lost as methane by the animal (*Methane_E*) is obtained by adding the methane produced in the rumen and that produced in hindgut (**27**). A reduction factor for methane formation (0.75) was taken from Danfaer (1998). Heat of combustion value per mol of methane is 0.890 MJ.

It is assumed in the model that a constant fraction of the gross energy intake is lost as urine energy (*Urinary_E*) (**28**), and the fractional rate constant for this equation is 0.04. The assumption that urinary energy losses are related to GE intake has been used previously in modelling purposes (Danfaer, 1998; Mills et al., 2001).

Energy lost as heat (*HE*) is the total heat production and is calculated as a function of gross energy intake (*GE_intake*) and milk yield (*MY*) plus heat produced due to pregnancy (*HE_preg*) (29). The equation for heat pregnancy in non-preg-

nant cows is estimated from literature data (Coppock et al., 1964; Holter et al., 1990; Gordon et al., 1995; Romo et al., 1996; Wilkerson et al., 1997; Sutton et al., 1998). *HE_Preg* is according to AFRC (1993) (30). The efficiency for growth of the concepta is 0.133 (AFRC, 1993).

Daily milk yield (MY) (31) can be given as an input to the model or calculated by an equation incorporated in FIRS. This equation is taken from Friggens et al. (1999) and reported originally by Emmans and Fisher (1986). In order to calculate the daily milk yield with this equation, information about the potential milk yield of the animal or the peak milk vield must be given to the model in addition to information about the parity number of the animal. With this equation it is possible to calculate potential milk yield for cows in their first, second and third or more parity. A total of four parameters, three coefficients and one scalar are used to calculate the equation. The b 1 coefficient describes the rate at which milk yield increases to peak, Go quantifies the degree of maturity of the milk producing system at calving, and c 1 describes the rate of decline in milk yield. a 1 is the milk yield scalar. Although the statistical analysis carried out by Friggens et al. (1999) shows relatively small effect of parity on the coefficients b 1 and Go, meaning that an average value could be used to predict potential milk yield across parities for the cited coefficients, all values for each coefficient and scalar in the equation are included in the FIRS.

The variable *Lactation_time* represents time in days from parturition and is used not only in the previous equation, but also for the estimation of many other variables in the model. This variable is calculated from the initial time of simulation in the model (*Ini_Lact_time*) that is given as input, by default this variable takes the value 1, meaning that the simulation starts at the first day in lactation. This initial time of lactation is updated in the model every 24 h of simulation time with the constant *Day1* (**32**).

Pregnancy has been proved to have a weak, but significant effect on milk yield in dairy cows (Coulon et al., 1995; Perochon et al., 1996). However, this effect is rarely taken into account in milk yield prediction models. The time at which pregnancy starts to have an effect on milk yield varies according to different authors and the importance given to that effect. Regardless of the milk yield potential of the cow or the time of conception, Coulon et al. (1995) have shown that the reducing effect of pregnancy can be detected from the 20th week of pregnancy. The equation for the lactation curve provided by Friggens et al. (1999) does not take explicitly into account the reducing effect of pregnancy on milk yield, because only milk records taken until 240 days post calving were considered for its construction. The effect of pregnancy was modelled in FIRS by the equation provided by Coulon et al. (1995) (**33**), which is added to the original equation of Friggens et al. (1999). Milk yield reduction due to the effect of pregnancy starts in the model at day 126 of pregnancy with the effect differing for primiparous and multiparous cows, and within this last group, for low-or-medium producing (< 32.5 kg milk d⁻¹) and high producing cows (> 32.5 kg milk d⁻¹). Pregnancy week (*PW*) (**34**) is computed in FIRS from the *Lactation_time* variable and the stage of lactation (in days) at the time of conception (*Conception_day*), a constant given as input to the model and set by default to day 92.

Daily energy retained in foetus (*Daily_Preg_E_Ret*) (**35** and **36**) is calculated according to the equation provided by AFRC (1993) based on information about time of pregnancy (*PW*) and calf birth weight (*Calf_Birth_W*). In the model, this last value is a constant that can be given as an input or a default value can be used (45 kg, a value for Holstein cattle given in AFRC, 1993).

Energy in milk is calculated as the product of MY and the energy value of milk (EV_Milk) (37). EV_Milk can be calculated by one of the three equations included in the model (38 to 40) depending on the information about milk composition available. The equations were taken from AFRC (1993). If no information about milk composition is available the model uses a constant value of 3.14 MJ kg⁻¹ of milk (41).

Determination of energy balance optimum and BCS factor

There are two aspects regarding body reserves that are related to the performance of the dairy cow. The first is the state or the level of body reserves in the cow and the second is the rate of change of body reserves during lactation (Maltz et al., 2001).

Friggens (2001) has stated the importance of the conceptual distinction between the level and the rate of mobilization of body reserves when analysing reproductive performance. He also stated that these two modifiers of parameters of reproductive performance should be combined additively. The same principle, but applied to nutritional aspects is applied in this model.

Determination of energy balance optimum

The level of body reserves or corporal condition of dairy cows changes during the lactation period at a similar pattern across many experiments (Garnsworthy and Jones, 1987; Pedron et al., 1993; Waltner et al., 1993; Ruegg and Milton, 1995; Gallo et al., 1996; Domecq et al., 1997; Friggens et al., 1998; Schroeder, 2000; Mao et al., 2001; Pryce et al., 2001). Body reserves are mobilized during the first part of lactation, then recovered through middle lactation and stabilized at nearly a steady state in late lactation. However, differences in the amount of reserves being mobilized have been observed due to breed (Schroeder, 2000; Mao et al., 2001), parity (Domecq et al., 1997; Schroeder, 2000; Mao et al., 2001), milk yield (Schroeder, 2000; Pryce et al., 2001), initial level of reserves (Garnsworthy

and Jones, 1987; Pedron et al., 1993; Ruegg and Milton, 1995) or feeding level (Friggens et al., 1998; Mao et al., 2001).

If this general pattern is consistent, it can be argued that a significant part of the mobilized reserves is not due to any of the factors mentioned above, but due to more basic species related genetic factors.

The biological basis and the supporting literature for this theory of cyclic nature of the body reserves in dairy cows have been clearly presented recently by Friggens (2001). In analysing this cyclic mobilization of body reserves, Friggens (2001) stated that body reserves in dairy cows are a safeguard for milk production at the beginning of the lactation, but its mobilization has negative consequences for the animal and the future offspring as lactation progresses. As a consequence of these concepts, targets of body fatness, which changes during the reproductive cycle, are assumed to exist in dairy cows.

In the FIRS, it is assumed that an optimal or reference level of body reserves or corporal condition (CC) curve exists for the whole lactation period of dairy cows. This optimal curve of CC should not only respect the needs of the animal for a high milk yield, but also be compatible with satisfactory achievements in reproductive performance and reduce to a minimum the risk of health problems. It is assumed that the difference between the CC value along that curve for two consecutive days, at any moment during the whole lactation period, is the optimal difference in terms of CC for that specific moment. If this daily optimal difference in CC units can be converted to energy units, the resulting value can be considered as the optimal daily energy balance for the dairy cow at that time of the lactation period.

A reference curve of body condition over the course of lactation has been published recently by Schroeder (2000). This reference curve has been formulated for high milk producing dairy cows (equal to or more than 9000 kg FCM y⁻¹) combined with acceptable fertility traits (interval between partum less than 380 days) and minimal health disorders. This optimal or reference curve has been included in the FIRS and calculated with equation (**46**). The curve is shown in Figure 1.

Original values of the optimum body condition in dairy cows were determined as mm backfat. Backfat is designated as the thickness of the subcutaneous fat depot that develops under the skin of the animal and can be determined by different methods, e.g., by ultrasound measurements. As a measurement of body condition, backfat is not usually available at farm level or in experiments, but a more common way to express body condition is by measuring body condition score (BCS). BCS is a subjective method and is indicative of the animal's nutritional status and body energy reserves. This method combines palpation (touching/feeling) and visual observation of the thickness of soft tissues in the lumbar and pelvic region. There are different scoring scales to measure BCS, but the most common scoring system in use is that proposed by Edmonson et al. (1989) with a scale from 1



Figure 1. Reference curve of optimal corporal condition during the lactation period measured as backfat or as body condition score (Scale 1 to 5). Adapted from Schroeder, 2000

(emaciated cows) to 5 (very fat cows) with 0.5 point divisions. The BCS system has been considered as a valid measurement of subcutaneous fat (Domecq et al., 1995; Schwager-Suter et al., 2000; Friggens et al., 2001). The optimal backfat values as proposed by Schroeder (2000) are converted into units of the BCS scale (Edmonson et al., 1989) (**45**).

The optimum energy balance $(E_bal_optimum)$ (42) in the model is a function of the optimum rate of change of body condition.

The optimum daily BCS change (*BCSC_optimum*) is determined as the difference between two BCS values estimated with a time distance of 24 h (43). This difference in terms of BCS units is converted to energy units by multiplying this value by the energy content per unit of BCS change. The energy equivalent to one unit of BCS change is variable depending on the amount of fat and protein being mobilized, and this in turn depends on the actual level of body reserves or body condition of the cow (Gibb et al., 1992). Various energy values can be found in the literature for gaining or losing of body tissue but little is published concerning the change of one unit of BCS. In the model, the energy value of one unit BCS change is calculated by the equation taken from Fox et al. (1999) for a cow with a shrunk body weight of 600 kg:

BCSC (MJ) = $(950.74 + 368.7 \times BCS \text{ optimum}) \times BCSC \text{ optimum}$

In order to calculate the optimum BCS change, the model uses an internal function of Powersim named *Delay* that allows to keep the information of the variable, in this case the value of *BCS_optimum*, of the previous day. The name of the delayed variable in all cases along the FIRS model corresponds to the variable to be delayed and the prefix $D_{,}$ i.e. $D_{BCS_optimum}$ is the delayed information of the variable *BCS_optimum*. Unless otherwise stated, the delay time of the delayed functions is 24 h.

Determination of BCS factor

The last variable in the equation determining E_diff_h is named Fac_BCS (47) and is included in order to account for the influence of initial (*Adjust_Ini*) and the actual (*Adjust_Actual*) BCS of the animal on feed intake. The theoretical basis for this factor has already been presented (see also Friggens, 2001). In the model this factor is modelled based on the condition of the cow at the start of the lactation, the optimal level of BCS during the lactation and the actual BCS of the animal as simulated by the model.

The effect of this factor would be divided in two according to the lactation time. At the beginning of the lactation this factor is mostly determined by Adjust Ini (48) that depend on the initial BCS of the dairy cow (*Initial BCS*) and this effect decreases as the lactation progresses, having almost no effect after the day 90 in lactation. The second term in equation (47) (Adjust Actual) reflects the influence of the actual optimum BCS, as determined by the previously mentioned curve (BCS optimum) and the actual value of BCS of the dairy cow as computed by the model (Upd BCS). Adjust Actual (49) at any point in lactation is estimated as the difference between the actual BCS of the animal (Upd BCS) and the optimum BCS of the animal (BCS optimum) at that time in lactation, times the energy content per unit of BCS (E BCS h). E BCS h is calculated in the same way as in equation 42, but using Upd BCS instead of BCS optimum (50). Upd BCS (51) is calculated once daily in the model at the beginning of each simulated day by the value of the variable during the preceding day (D Upd BCS) plus the change in BCS during the day, $(BCSC \ M)$ (52) calculated by the model from the energy balance (MJ d^{-1}). This equation (52) as in the case of equations (42) and (51) is estimated using the values of the energy content per unit of change of BCS as proposed by Fox et al. (1999). The variable (Sigm 1) (53) makes sure that the effect of Adjust Actual is not constant across the whole lactation period, but increases in a sigmoid fashion with a full effect at about 200 days in lactation.

Initial liveweight (*Body_weight*) is given as an input to the model and then is updated daily (*Upd BW*) using the variable *E balance* and a net energy value of

17.3 MJ kg⁻¹ liveweight loss and 20.9 MJ kg⁻¹ liveweight gain. These values for liveweight loss and gain were reported by Gibb et al. (1992) for Holstein-Friesian cows. They were determined from a serial slaughter and carcass analysis in lactating dairy cows, which included different proportions of fat and protein mobilized or gained during the period of analysis. Upd_BW is used in the model for the determination of the comminution rate constant from large to small particles and of the liquid passage rate constant.

The rumen digesta load

The variable *Rumen_load* (55) represents the rumen digesta load in the model, which is the sum of all NDF fractions in the rumen. The NDF fraction of the rumen digesta has been used to represent the digesta load in other models of feed intake prediction (Williams et al., 1989; Fisher and Baumont, 1994; Fisher, 1996; Chilibroste et al., 1997; Tess and Kolstad, 2000).

Feed intake regulation

Once both elements of the Weston's theory, the energy deficit and the rumen digesta load, have been defined by the model, the next step is the integration of them into an equation describing the regulation of feed intake. In the FIRS this is represented by a group of equations (from 56 to 62).

An upper limit to accommodate digesta in the rumen has often been mentioned as the real factor deciding the end of a meal and consequently determining feed intake in dairy cows. A physical upper limit in rumen capacity exists and is determined by the total volume of the rumen, but as this space is always partially filled with digesta, a more precise word is rumen digesta load than rumen fill.

In most cases, this upper limit to accommodate digesta has been defined as a constant. Mertens (1987) proposed that until the cow covers its energy requirements, the rumen fill remains constant and only then decreases. Rejecting the concept of constant fill, Fisher et al. (1987) proposed a curvilinear relationship between rumen fill and energy balance. A logistic model describing maximum and minimum rumen fill modulated by palatability and energy balance was proposed by Faverdin et al. (1995). Variable upper and lower limits to rumen fill were also used by Danfaer (1998) and modelled according to the absorbed energy, body weight and the expected milk yield of the dairy cow.

Values for rumen digesta load or more specifically NDF rumen digesta load are available in the literature related to a different variables (i.e. feed intake, time from feeding, type of diet, energy intake, etc.). However, relationships between NDF rumen digesta load and energy deficit as proposed by Weston are scarce. But no values could be found in the literature relating energy difference as proposed

in FIRS and NDF rumen digesta load. As a consequence the curve describing the upper limit of NDF rumen digesta used in the present model is totally theoretical, but based on sound values.

The upper limit of NDF digesta load in the rumen (*Upper*) (**56**) is determined in the FIRM model as a function of the energy difference (E_diff_h) determined previously. This relationship is shown in Figure 2.

The constants *Alfa1* to *Alfa5* determine the shape of the curve. The minimum value of the upper limit is set by the constant *Alfa1* (4.15 kg NDF), while *Alfa2* (4 kg) is the difference between the minimum and the maximum value that *Upper* can reach. Therefore, the maximum value of rumen digesta load in the model is 8.15 kg of NDF.

The lower limit of the digesta load in the model (*Lower*) (57) is given as a constant difference from the upper limit, in this case 0.6 kg of NDF. A constant difference between upper and lower limits was also used by Danfaer (1998) in his whole animal model.

Minimum and maximum values adopted for the mentioned limits are well within the range of values of NDF rumen content normally found in the literature. However, lower or higher values than the minimum (3.55 kg NDF) or maximum (8.15 kg NDF) values adopted in FIRS have been reported occasionally in the literature (Okine et al., 1991; Robinson et al., 1991; Lund, 2002).



Figure 2. The relationship between energy difference as determined by the model and the upper limit of rumen NDF load

When used as maximum rumen fill in the calculation of feed intake, different values were adopted. Mertens (1987) has estimated an NDF capacity of 6.6 kg for a cow with a body weight of 600 kg whereas a value of 5.5 kg of NDF was the value used by Madsen et al. (1994), close to the 5.4 kg used by Chilibroste et al. (1997) in his simulation model. With a few exceptions these values were fixed and are close to the middle point of the curve of NDF rumen load used by FIRS.

The decision between eating or not in the model is made through the equations **58** to **62**, taken from Danfaer (1998). A schematic presentation of these equations is presented in Figure 3. In this graph, the cow stops eating when the rumen load (Line 1) is reaching the upper limit (NE Section) and is prevented from eating until the decreasing rumen digesta load reaches the lower limit. When this occurs,



E = Period of time when the dairy cow is eating

NE = Period of time when the dairy cow is not eating

Figure 3. Rumen load regulation. Graphical representation of rumen digesta load and limits from a simulation in Powersim and results of the variables regulating feed intake in FIRS (see text)

the eating starts (E Section) and continues until the upper limit is reached again. Lines 2 and 3 represent the upper and lower limit of digesta load, respectively. As shown in the graph, the upper limit and as a consequence the lower limit are not constant during the simulation period because the limits are dependent on E_diff_h . The rate of eating (*Eating*) in the FIRS model is a constant with a value of 3.3 kg DM h⁻¹. Danfaer (1998) in the Karoline model has made this rate variable and controlled by absorbed energy and expected milk yield.

Preliminary behavioural evaluation

A preliminary assessment of the behaviour of the model was carried out running FIRM with a typical diet as input. The diet was composed of grass silage and concentrates in the proportion of 65 and 35%, respectively. The chemical composition of this diet used was (expressed as percentage of DM): NDF 42, crude protein 20, starch 8, sugars 3.5 and ash 10.5. A dairy cow in its third parity weighing 600 kg with an initial body condition score of 3.2 and two different milk yields (Low = 7000 or High = 9000 kg FCM y⁻¹) was used as input for the model.



Figure 4. (a, b and c). Predicted values of dry matter intake, milk yield and body condition score during the lactation period for a cow producing 7000 (\Box) or 9000 (\bullet) kg of FCM y⁻¹

Results produced by FIRM for the whole lactation period and for both milk yields are shown in Figure 4 (a, b and c). Figure 4a shows dry matter intake predicted by the model for the Low and High milk yield. Typical curves are predicted with the highest intake for the cow producing more milk. Both milk production curves simulated by the model with peaks around day 35 in lactation are shown in Figure 4b. Curves of body condition score for Low and High milk production (Figure 4c) are consequences of the different intakes and milk yields shown in Figures 4a and 4b, respectively. Minimum BCS are obtained later in lactation for the cow with high milk yield than for the cow with low milk yield.

CONCLUSIONS

The aim of this work was to develop a dynamic, mechanistic and deterministic model of feed intake regulation in which the rumen function and the energy transactions representing the physical and metabolic regulation in the dairy cow are integrated. The traditional concept of intake regulation was rejected and the present model is based on a sound conceptual model of feed intake regulation, which has not previously been implemented in a working model.

The bi-phasic regulation theory states that either one or the other regulates the feed intake process whereas the present model regulates the feed intake process using both the physical and the metabolic signals as determinants of feed intake at every moment. Discrimination between physical or metabolic regulation, at least in the classical approach, is not possible with the present model.

Forage constraints acting mainly at the level of digesta flow are included in the model by the incorporation of a previously developed rumen model. Body reserves, both the absolute level and the rate of mobilization are integrated in the regulation of feed intake.

A preliminary evaluation of the model behaviour with a typical diet and for cows with different milk yield capacities has resulted in reasonable and expected simulated values for feed intake and body condition score. A further application and evaluation of the present model will be given in a forthcoming paper.

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STRESZCZENIE

Dynamiczny model regulacji pobrania paszy dla krów mlecznych. Opis modelu

W pracy przedstawiono dynamiczny, mechanistyczny i deterministyczny model regulacji pobrania paszy przez krowy mleczne. Model ten bazuje na współzależności między funkcjonowaniem żwacza a przemianami energii, uwzględniającymi pobranie paszy. Model zawiera dwa wewnętrznie powiązane submodele: submodel żwacza (RS) bazujący na już istniejącym modelu żwacza i submodel regulacji pobrania pasz (F1RS). Na podstawie RS obliczone jest obciążenia żwacza (w kilogramach NDF). FIRS nie tylko opisuje regulacje pobierania paszy, lecz także trawienie, wchłanianie i wypływ składników pokarmowych ze żwacza. W tym modelu przemiany energii są związane z symulowaną różnicą między zdolnością wykorzystania energii a pobraniem energii metabolicznej. Wykorzystanie energii obejmuje nie tylko energię na potrzeby bytowe i na produkcję mleka u zwierzęcia, ale również energię potrzebną do zaspokojenia genetycznie uwarunkowanych rezerw organizmu. Rezerwy organizmu, zarówno wartość względna, jak i tempo odkładania, uwzględniane są w modelu regulacji pobrania paszy. Wstępna ocena modelu dla typowej dawki i pobrania wykazała, że prognozowane wartości są mniejsze od oczekiwanych w zakresie pobrania paszy, kondycji i masy ciała.

APPENDIX

E diff $h = E$ balance - E bal optimum + Fac BCS, <i>MJ</i> h^{-1}	(1)
E balance = ME - HE- Daily Preg E Ret/24 – Milk E/24, MJh^{-1}	(2)
$\overline{ME} = GE$ intake - Faecal $\overline{E} - Methane E - Urinary E, MJ h^{-1}$	(3)
GE intake = DMI × GE, $\overline{MJ} h^{-1}$	(4)
Faecal E = Faecal C × 0.546 + Faecal N × 23.7 / 11.423, $MJ h^{-1}$	(5)
Faecal $C = NDF$ SI + OtherCHO SI + Sugar starch HG	
+ Lipid HG + Protein HG \times 3.8 - (Ab AC HG + Ab PR HG	
+ $Ab \overline{BU} HG + CH4 \overline{HG} + CO2 \overline{HG}$, mol C h ⁻¹	(6)
NDF SI = NDF Passage × CCCHO / 24, mol C h^{-1}	(7)
OtherCHO SI = P OCL + P OCS + O MIC \times 0.0937, mol C h ⁻¹	(8)
Sugar starch $HG = Sugar SI + Starch SI - Glucose, mol C h^{-1}$	(9)
Sugar SI = P SU + O MIC × 0.1817 × 3 / 51, mol C h^{-1}	(10)
Starch SI = ST passage × CCCHO / 24 + O MIC × 0.1351, mol C h^{-1}	(11)
Glucose = (Sugar SI + Starch SI) × 0.884, mol C h^{-1}	(12)
Lipid HG = Lipid SI - Fatty acids, mol C h^{-1}	(13)
Lipid SI = P LI + O MIC × 0.1817 × 48 / 51, mol C h ⁻¹	(14)
Fatty acids = Lipid $\overline{SI} \times 0.833$, mol C h ⁻¹	(15)
Protein HG = Protein SI + Endog protein - Amino acids, mol Nh^{-1}	(16)
Protein $SI = P A3 + \overline{P} A2L + P \overline{A2S} + P A1L + \overline{P} A1S + O MIN,$	
$mol N \overline{h^{-1}}$	(17)
Endog protein = DMI × K EP, mol N h^{-1}	(18)
Amino acids = Protein SI \times 0.735, mol N h ⁻¹	(19)
Fermentable $HG = NDF$ SI + OtherCHO SI + Sugar starch HG +	
(Protein HG-Endog protein) \times 3.8, mol Ch^{-1}	(20)
Ab AC HG = Fermentable HG \times 0.0813, mol C h ⁻¹	(21)
Ab PR HG = Fermentable HG \times 0.0355, mol C h ⁻¹	(22)
Ab \overline{BU} HG = Fermentable HG × 0.0242, mol C h ⁻¹	(23)
$CH\overline{4}$ $H\overline{G}$ = Fermentable $H\overline{G} \times 0.0158$, mol C h ⁻¹	(24)
$CO2^{HG} = Fermentable^{HG} \times 0.0382$, mol C h ⁻¹	(25)
Faecal N = Protein HG - 0.184, mol N h^{-1}	(26)
Methane $E = (Ab CH4 + CH4 HG) \times 0.75 \times 0.890$, <i>MJ h</i> ⁻¹	(27)
Urinary $E = K$ UE × GE intake, $MJ h^{-1}$	(28)
$HE = HE Preg / 24 + GE intake \times (37.813 - K HE * MY) / 100), MJ h^{-1}$	(29)
HE Preg = Daily Preg E Ret × (1 / 0.133 – 1), $MJ d^{-1}$	(30)
$MY = \{a \ 1 \times [EXP(-EXP(Go-b \ 1 \times Lactation \ time))]$	
× [EXP(-c 1×Lactation time)] + MY Preg Red}, $l d^{-1}$	(31)
Lactation_time = IF (TIME<= Day1, Ini Lact time, INT (TIME - Day1) /	. /
$Day1) + Ini_Lact_time + 1-TIMECYCLE (0, Day1)), d$	(32)
MY_Preg_Red = (-e ^{-aMR} × [(PW – 18) × e ^{-bMR * PW}]), $l d^{-l}$	(33)

PW = (Lactation time - Conception day) / 7, week	(34)
Daily Preg E Ret = $0.025 \times \text{Calf Birth W} \times$	Ì,
(Total Preg E Ret \times 0.0201 \times EXP(-0.0000576 \times PW \times 7) <i>MJ d</i> ⁻¹	(35)
Total Preg E Ret = $10^{(151.665 - (151.64 \times EXP(-0.0000576$	Ì,
$\times PW \times 7)), \overline{MJ}$	(36)
Milk $E = MY \times EV$ Milk, $MJ d^{-1}$	(37)
EV $\overline{\text{Milk}} = 0.0384 \times \text{Butterfat}$ $\overline{\text{Milk}} + 0.0223 \times \text{Protein}$ $\overline{\text{Milk}} + 0.0199 \times \text{Milk}$	
Lactose Milk-0.108, $MJ l^{-1}$	(38)
EV Milk = $0.0376 \times$ Butterfat Milk+ $0.0209 \times$ Protein Milk+ 0.948 , MJ l ⁻¹	(39)
EV Milk = $0.0406 \times \text{Butterfat}$ Milk+1.509, <i>MJ l</i> ⁻¹	(40)
$EV_{Milk} = 3.14, MJ l^{-1}$	(41)
E bal optimum = (BCSC optimum \times (BCS optimum	
$\times 368.7 + 950.74)) / 24, MJ h^{-1}$	(42)
BCSC optimum = BCS optimum - D BCS optimum	(43)
D BCS optimum = DELAYPPL (BCS optimum, 24,0)	(44)
BCS optimum = RBF Optimum $\times 0.1+1$	(45)
RBF Optimum = Lact1-Lact2 × Lactation time + Lact3	
×Lactation time^2 -Lact4 ×Lactation time^3 + Lact5	
\times Lactation time^4, mm	(46)
Fac BCS = - Adjust ini + Adjust Actual, MJh^{-1}	(47)
Adjust ini = $(2.125 - 0.625 \times \text{Initial BCS}) \times \text{EXP}(\text{-Cte } 137 \times (\text{TIME}))$	
MJh^{-1}	(48)
Adjust Actual = (E BCS $h \times (Upd BCS - BCS optimum))$	
/ K BCS × Sigm1, $\overline{MJ} h^{-1}$	(49)
E BCS h = (Upd BCS × 368.7 + 950.74)/24, MJ h^{-1}	(50)
$\overline{Upd} BCS = D Upd BCS + BCSC M$	(51)
\overrightarrow{BCSC} M = (\overrightarrow{E} balance / (950.74 + 368.7 × D Upd BCS)	(52)
Sigm1 = $1-EXP(-cte1 \times Lactation time^Cte3)$	(53)
Rumen load = TPR / 37.037, kg	(54)
$TPR = \overline{C}1L + C1S + C2L + C2S, mol C$	(55)
Upper = $alfa1+alfa2 \times EXP(-alfa3 \times (E diff h+alfa5)^alfa4), kg$	(56)
Lower = Upper – Diff, kg	(57)
Load $\text{RegA} = \text{IF}(\text{Der Load} < 0 \text{ AND Rumen load} < \text{Lower}, 0, 1)$	(58)
Load $\text{RegB} = \text{IF}(\text{Der Load} \ge 0 \text{ AND Rumen load} < \text{Upper}, 0, 1)$	(59)
Load_Reg = Load_RegA ×Load_RegB	(60)
$DMI = IF(Load_Reg = 0, Eating, 0), kg DM h^{-1}$	(61)
Feed_intake = $24 \times \text{INTEGRATE (DMI)} / \text{TIME}$, kg DM d ⁻¹	(62)